

Original Article

Adaptive radiation, ‘taxon murk’, and the reality of early burst speciation: an example from Australia’s scincid lizards

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ABSTRACT

Early burst patterns of speciation—the disproportionate concentration of speciation events early in the history of a radiating clade—are predicted under some models of adaptive radiation. Using time-calibrated phylogenetic trees, researchers have inferred evidence of an early burst for a wide range of organisms. However, the interpretation of these patterns can be fraught with controversy, because taxonomic and sampling biases—a phenomenon we refer to as ‘taxon murk’—can lead to apparent decelerations in the rate of speciation through time. Using Australia’s diverse sphenomorphine scincid lizards as a model, we tested whether multiple forms of tip-level uncertainty, including taxonomic undersampling and lag time for species recognition, could bias inference of speciation rates. To explore the impacts of taxon murk on diversification inference, we constructed a phylogenomic tree for 1941 individuals spanning 211 nominate species of sphenomorphines, including extensive sampling of intraspecific diversity. We found that the Australian sphenomorphine radiation is characterized by a robust early burst pattern that cannot be explained by uncertainty in the nature of tip units. These results are surprising, because extinction-mediated turnover should erode the signal of early burst speciation from molecular phylogenies. We provide a possible resolution to this paradox and consider the implications of our findings for continental radiations more generally. However, profound gaps in our knowledge of sphenomorphine behaviour and ecology limit our ability to test whether sphenomorphine macroevolutionary dynamics are consistent with paradigmatic patterns observed in better-studied radiations.

Keywords: adaptive radiation; diversification; phylogenetics; species delimitation; cryptic species; sphenomorphine lizards; phylogenomics; target capture; ddRAD

INTRODUCTION

Understanding the causes of evolutionary diversification remains a central challenge in biology. Even within a particular geographical theatre and ecological context, evolutionary radiations frequently show strikingly disparate outcomes among clades, with some clades becoming far more diverse in species

and phenotypes than others. Fundamentally, understanding evolutionary diversification requires us to characterize its tempo and mode through time. For most groups of organisms, we can only reconstruct this history through the use of dated phylogenetic trees. Such phylogenies are our best hope to infer the rate at which new species form, the extent to which those rates differ

among lineages, and, potentially, the rate at which they go extinct (Nee *et al.* 1994, Title and Rabosky 2019). There has thus been widespread interest in developing methods to reconstruct diversification using dated phylogenies and in applying those methods broadly to understand how and why life has become so diverse (Morlon 2014, Rabosky 2014, Maliet *et al.* 2019).

The interest in these methods has also led to active debate about their efficacy, with studies showing that these methods cannot always discriminate across competing models and sometimes misestimate key model parameters (Louca and Pennell 2020, Kopperud *et al.* 2023). These debates have revealed profound limits to inference based on some widely used methods (Maddison 2006, Maddison and FitzJohn 2015, Rabosky and Goldberg 2015), while also spurring the development of more robust frameworks for diagnosing and accommodating model inadequacy (Beaulieu and O'Meara 2016, Harvey and Rabosky 2018). Yet far less attention has been given to the ‘data side’ of diversification rate inference—specifically, how accurately the dated phylogenetic tree captures the true evolutionary history of a clade. While some studies have addressed the extent to which diversification inferences are robust to phylogenetic uncertainty (Rangel *et al.* 2015), tree construction biases (Revell *et al.* 2005, Duchêne *et al.* 2017), and gene tree variance (Burbrink and Pyron 2011), most empirical studies assume that the uncertainty in diversification analyses is likely to come from the inference machinery itself. Typically, these studies assume the input data are fixed and account for uncertainty by confirming

diversification inferences are robust across a posterior or bootstrapped sample of trees (Biswas and Karanth 2024, Marcondes and Douvas 2024).

One potential and underappreciated source of uncertainty is the taxonomy that underlies the diversification analysis (Ruane *et al.* 2014, Freeman and Pennell 2021, Utami *et al.* 2022, Frateles *et al.* 2024, Tavares *et al.* 2024), which we describe here loosely as ‘taxon murk’ (Table 1). By ‘taxon murk’, we refer to multiple sources of variability that affect the number, nature, and properties of the species-level units that are typically used as inputs into higher level analyses of species diversification patterns from phylogenetic trees. As such, taxon murk is conceptually similar to the notion of ‘tip fog’, as coined by Beaulieu and O’Meara (2024) to describe uncertainty in species trait values used for downstream comparative analyses. Perhaps the most familiar form of ‘taxon murk’ is incomplete sampling, or the failure (or inability) to sample all known species-level lineages. Several methods account for this source of error (Chang *et al.* 2020) by assuming that the true number of species is known and, more significantly, that one can model the process that produced the set of sampled species given the ‘known’ phylogeny. However, whether known but unsampled species represent a phylogenetically random, overdispersed, or underdispersed subset of all species in a clade can have substantial consequences for diversification inference (Pybus and Harvey 2000, Cusimano and Renner 2010, Höhna 2014).

Table 1. Possible sources of ‘taxon murk’ that might affect diversification inference.

| Source of taxon murk | Description | Effect on inference of rate variation through time | Effect on inference of rate variation across clades | Example from this study |
|--|---|---|---|---|
| Incomplete sampling | True number of species is known but not all species are sampled; we cannot always model these missing taxa adequately | Infer an overall slowdown in speciation rates through time | Infer greater speciation rate for better sampled clades relative to lesser sampled clades | Of the currently recognized species, we have sampled 76% in our phylogeny |
| True diversity is unknown | Either fundamentally new species remain to be discovered with more field-based surveys and/or cryptic diversity within species has yet to be fully described | Infer an overall slowdown in speciation rates through time | Infer greater speciation rate for better characterized clades relative to lesser characterized clades | Named morphological species often consist of cryptic lineages exhibiting nearly as much divergence as morphological species (Fig. 1) |
| Differences in taxonomic practice across clades | Either taxonomic effort or the criteria used to define taxonomic units differs across clades | Infer acceleration of speciation rates in ‘oversplit’ clades towards the present | Infer greater speciation rate for ‘oversplit’ clades relative to ‘undersplit’ clades | None noted |
| Evolutionary dynamics of taxonomically relevant characters differ among clades | Difference in evolution of key taxonomic traits varies across clades, such that even with consistent taxonomic practice, named species are not comparable across clades | Infer acceleration of speciation rates in clades with labile taxonomic traits towards the present | Infer greater speciation rate for clades with more labile taxonomic traits relative to clades with less labile traits | Many <i>Ctenotus</i> species were defined by colour pattern, which is particularly labile in the <i>inornatus</i> group and has led to messy taxonomic boundaries (Supporting Information Table S2) |
| Protracted speciation | Most taxonomies typically do not include the most recent speciation events (‘incipient species’) | Infer an overall slowdown in speciation rates through time | None noted | Many of our species contain within-species population-level lineages, which might be future ‘good species’ (Fig. 1) |

Another key source of taxon murk involves the extent to which true lineage diversity is recognized by existing taxonomic schema. Some clades have simply been insufficiently studied, such that field-based surveys and further sampling will continue to uncover species that are fundamentally new to science (Bini *et al.* 2006). However, the potential for unrecognized diversity exists even within reasonably well-studied groups. Many traditional taxonomies are based upon visual examination and comparison of organismal morphology, especially those characteristics that are readily catalogued and described by human observers. For clades where lineages might diverge in traits that are less readily accessible (e.g. pheromone composition, physiology), existing taxonomies often inadequately describe ‘true’ species-level diversity, and genetic data often reveal the presence of morphologically cryptic lineages within traditionally defined species (Bickford *et al.* 2007, Pfenninger and Schwenk 2007, Zozaya *et al.* 2019).

By underestimating the true lineage-level diversity of a clade, unrecognized cryptic diversity is ultimately a form of undersampling. Notably, this source of taxon murk might lead to apparent (=spurious) slowdowns in the rate of speciation through time (Pybus and Harvey 2000, Freeman and Pennell 2021). Likewise, variation in the magnitude of undersampling among clades might lead to apparent among-lineage variability in the rate of diversification, especially when researchers fail to recognize that focal clades differ in the proportion of undescribed species they contain. While such variability can arise from biases in taxonomic effort, it can also arise from clade-specific variation in the evolution of traits typically used in traditional taxonomies. For example, species boundaries in birds are often defined by differences in plumage, leading to a bias against species description in bird clades showing less labile plumage evolution relative to clades with more labile plumage coloration (Freeman and Pennell 2021).

Taxon murk can also emerge automatically from the protracted nature of speciation itself. In some circumstances, lineages can evolve evolutionary distinctiveness very rapidly (Wood *et al.* 2009, Lamichhaney *et al.* 2018), but typically, speciation is seen as a continuous process (Darwin 1859). Populations often have a substantial waiting time before they evolve the attributes typically considered to characterize ‘good species’, such as ecological and phenotypic divergence and intrinsic reproductive isolation (Avise and Walker 1998, Weir and Schlüter 2007, Etienne *et al.* 2014). As a consequence, some of the population divergences of today are in fact the interspecific divergences of tomorrow. Because we do not have access to the future, we cannot infer from present-day data which of intraspecific divergences or incipient species will ultimately represent ‘good’ speciation events (Dynesius and Jansson 2014). However, our inability to recognize these recent speciation events might lead us to mistakenly infer temporal slowdowns in speciation rates (Weir 2006, Etienne and Rosindell 2012).

In this article, we utilize dense phylogenomic sampling of a model vertebrate clade—Australia’s sphenomorphine lizards—to explore the effects of taxon murk on inference of species-level diversification patterns. With nearly 280 taxonomically recognized species, the sphenomorphines represent Australia’s most species-rich vertebrate radiation. They are common members

of the ecological communities in which they occur, comprising a substantial proportion of total lizard diversity and abundance at many sites (Pianka 1986, 2014, Morton and James 1988, Rabosky *et al.* 2011). Previous analyses of diversification dynamics in sphenomorphines have identified two general patterns. First, the genera *Ctenotus* and *Lerista*—which are the most species-rich genera in the group, accounting for 73% of species—have speciation rates that are nearly double in relation to the rest of the clade (Rabosky *et al.* 2007b, 2014a). Second, speciation rates in the group show an ‘early burst’ pattern, whereby rates were highest during the early phase of the radiation and subsequently decelerated through time (Rabosky *et al.* 2014a). Similar patterns appear to characterize many other radiations (Nee *et al.* 1992, Lovette and Bermingham 1999, McPeek 2008) and are consistent with ecological constraints on clade diversification, potentially arising from declining ecological or geographical space as species diversity increases (Sepkoski 1978, Gavrilets and Vose 2005, Rabosky 2009). We caution, however, that phylogenetic diversification patterns are not reliable indicators of specific causal processes, such as adaptive radiation (Givnish 2015, Rabosky and Hurlbert 2015). In particular, we recognize that early burst patterns, or periods of rapid speciation more generally, might have little to do with the ecological diversification traditionally associated with adaptive radiation (Moen and Morlon 2014, Givnish 2015).

It is unclear, however, to what extent sources of taxon murk might have contributed to this apparent early burst scenario. Genetic data have challenged traditional views of sphenomorphine taxonomy, raising questions about the accuracy of diversification inferences based on those taxonomic units. The vast majority of sphenomorphine taxa were described solely based on morphology, including traits such as body size and shape, scalation patterns, colour pattern, and degree of digit and limb loss (Storr 1979, 1981, Cogger 2014). In some cases, the addition of range-wide genetic sampling has uncovered highly diverged, putatively cryptic lineages within morphologically defined species, a few of which have been subsequently named and described (Rabosky *et al.* 2017, Prates *et al.* 2022a). On the other hand, genomic data have also revealed that these morphological traits—which have traditionally been assumed to be relatively stable within species (Storr *et al.* 1999)—are highly labile, resulting in taxonomic uncertainty within several species complexes (Rabosky *et al.* 2014b, Prates *et al.* 2024). Ultimately, these genomic data have shown that some morphologically defined species and subspecies lack the evolutionary coherence and distinctiveness as to warrant continued recognition (De Queiroz 1998, Rabosky *et al.* 2014b, Farquhar *et al.* 2024, Prates *et al.* 2024), potentially creating another source of taxon murk that could influence diversification estimates.

To test the influence of taxon murk on speciation rates as inferred from phylogenetic trees, we constructed an inclusive phylogeny of 1941 individuals and 211 nominal species by sampling both intraspecific and interspecific divergences across the sphenomorphine radiation. We then apply four taxonomic frameworks to this phylogeny (Table 2) that potentially capture different sources of taxon murk (Table 1). Across these four frameworks, we ask two questions. First, how stable are inferences about tip-level speciation rates—and about rate

differences among clades—with respect to taxon murk? Second, how robust are inferences about the tempo of speciation and lineage accumulation through time with respect to taxon murk? In particular, we test whether, under these alternative taxonomic frameworks, we still recover a pattern of increased speciation rates at the base of the sphenomorphine radiation followed by a subsequent slowdown, as indicative of an ‘early burst’ speciation pattern.

METHODS

Overall approach

Our primary goal was to understand how taxon murk can affect the characterization of phylogenetic diversification patterns (Table 1), using a large empirical dataset as a test case. We built an individual-level phylogeny that we then subsampled to create alternative taxonomic frameworks that encompassed multiple sources of uncertainty about the nature of the tip units. This approach ensures that any biases or errors in phylogenetic reconstruction are shared across the phylogeny for each provisional delimitation scheme. To build this common phylogenetic framework, we created a scaffolded inference approach that is based on ~5000 target-capture loci (Singhal *et al.* 2017b), the mitochondrial DNA (mtDNA) locus *cytochrome b*, and ~2000 double-digest restriction aided digest loci (ddRAD; Peterson *et al.* 2012). Ultimately, this approach allowed us to generate a phylogeny spanning 1941 individuals across 211 of the nearly 280 currently recognized species in the group (Supporting Information Table S1). We refer to this phylogeny as the ‘synthetic’ phylogeny.

We then subsampled the synthetic phylogeny to represent four distinct taxonomic frameworks that differ in their treatment of hypothesized species-level units (Table 2). Because these

delimitations differ in the number and phylogenetic distribution of putative species, we might expect differences in diversification rate inferences drawn from phylogenies matching each delimitation. See ‘Defining provisional taxonomic frameworks’ below for further details on how we defined these frameworks.

Data collection and processing

We sampled as extensively across the sphenomorphine phylogeny and across species’ geographical range as possible. For use as outgroups, we included eight species. Each ingroup individual ($N = 1941$) was sequenced for either ddRAD, mtDNA, and/or phylogenomic target-capture data. In total, 57% of individuals ($N = 1120$) were sequenced for ddRAD data, 87.8% ($N = 1706$) for mtDNA, and 15.2% ($N = 296$) for target-capture data; 50% of individuals were sequenced for more than one locus type, and 61% were sequenced across the nuclear genome (Supporting Information Fig. S1).

The majority of the ddRAD data have been previously published (Singhal *et al.* 2017a, 2018a, Prates *et al.* 2022b). We analysed these data with respect to their operational species designations, as discussed below under ‘Defining provisional taxonomic frameworks’. For each operational species, we used an iterative reference-based approach to convert our base genome (*Ctenotus leonhardii*) into a pseudo-reference genome for the species (Sarver *et al.* 2017). To do so, we mapped reads to the genome using bwa v.0.7.17 (Li 2013), called variants using bcftools v.1.10.2 and samtools v.1.16.1 (Li *et al.* 2009), and then mutated the base genome to incorporate any mutations present at >0.5 frequency. We repeated this three more times to generate the final pseudo-reference genome. We then mapped reads to the pseudo-reference genome, called variants, and retained all invariable and variable sites present at $\geq 5x$ depth. This approach

Table 2. The four taxonomic frameworks used in this study to test the potential effects of ‘taxon murk’ on our understanding of two key diversification patterns in the sphenomorphine lizards: (i) a nearly doubling of speciation rate at the ancestor of the two most species-rich genera *Ctenotus* and *Lerista* and (ii) a slowdown in diversification rates through time, as measured by the gamma statistic (γ).

| Taxonomic framework | Attempting to resolve taxon murk due to: | Description | Sampled taxa | Identified increase in speciation at base of <i>Ctenotus</i> & <i>Lerista</i> ? | Identified slowdown in diversification through time? |
|-----------------------|--|--|--------------|---|--|
| Morphological species | This taxonomic framework serves as our baseline | Includes those species defined by morphological data only; this is nearly synonymous with the currently recognized taxonomy | 200 | True | True ($\gamma = -8.1$) |
| Operational species | True diversity is unknown | Reflects our best understanding of species boundaries based on genetic, phenotypic, and geographical analyses | 251 | True | True ($\gamma = -10.7$) |
| Incipient species | Protracted speciation | Includes population-level lineages found within operational species; these lineages are thought to reflect ‘incipient species’ | 402 | True | True ($\gamma = -3.2$) |
| Threshold species | Differences in taxonomic practice across clades; evolutionary dynamics of taxonomically relevant characters differ among clades; protracted speciation | Applies a single age threshold below which all lineages are collapsed into one species-level taxon | 258 | True | True ($\gamma = -11.3$) |

allowed us to identify homologous sites across individuals across ~5 Myr of divergence, while also avoiding some of the technical artefacts associated with ddRAD data (e.g. allelic dropout, inflated terminal branch lengths; DaCosta and Sorenson 2016).

Our mtDNA data consisted of the coding sequence *cytochrome b*. Most sequences have been previously published (Rabosky *et al.* 2014b, Prates *et al.* 2022a, 2023, 2024, Farquhar *et al.* 2024). We prepared these data for analysis by generating an alignment with mafft v.7.453 (Katoh *et al.* 2009) and editing the coding sequence for gaps using Geneious v.2022.2.2 (Kearse *et al.* 2012).

We collected the target-capture data using two complementary approaches. For 93 individuals, we sequenced 394 anchored hybrid enrichment (AHE) loci (Lemmon *et al.* 2012). To do so, we extracted DNA using a Qiagen DNeasy Kit, quantified quality running an agarose gel, and used a Qubit v.2 fluorometer to quantify concentrations. The Center for Anchored Phylogenomics at Florida State University then prepared libraries and performed target capture using methods outlined in Lemmon *et al.* (2012). The enriched libraries were pooled into groups of ~16 samples and sequenced across two 250 paired-end lanes of a HiSeq2500 at the Translational Laboratory at Florida State University. For the remaining 203 individuals, we sequenced a 5453-locus target set that includes AHE loci, ultraconserved elements, and markers traditionally used in squamate phylogenetics (Squamate Conserved Loci; SqCL) (Faircloth *et al.* 2012, Singhal *et al.* 2017b). Of these 203 individuals, 31% were previously published (Grundler *et al.* 2019, Title *et al.* 2024); full details on data collection are available in those studies.

We processed the two sources of target-capture data using the same pipeline (Singhal *et al.* 2017b). Briefly, we trimmed adapter sequence from reads using Trimmomatic v.0.36 (Bolger *et al.* 2014), merged overlapping reads using PEAR v.0.9.10 (Zhang *et al.* 2014), and then assembled reads using Trinity v.2.3.2 (Grabherr *et al.* 2011). We annotated assemblies using blat v.36x1 and exonerate v.2.2.0 (Kent 2002, Slater and Birney 2005). Then, we generated multispecies alignments across all loci using mafft v.7.294b. Finally, we trimmed alignments to remove any alignment position that had less than 30% occupancy, to remove any sequences that were shorter than 300 bp, and to remove any loci for which we recovered fewer than 5% of sequenced individuals.

Phylogenetic estimation

We attempted to build a synthetic alignment across ddRAD, mtDNA, and target-capture loci, but allelic dropout for the ddRAD data was too high across the nearly 20 Myr of evolution spanned by our sampling. Instead, we used an approach inspired by Upham *et al.* (2019) and Title *et al.* (2024), in which we inferred the phylogeny in clade-level groups and then grafted these clades into a backbone.

First, we inferred our backbone based on the target-capture data. We concatenated our trimmed alignments of both AHE and SqCL loci and then inferred a tree using IQ-TREE v.2.2.0 (Minh *et al.* 2020). We calculated nodal support through Shimodaira–Hasegawa approximate likelihood ratio tests (SH-aLRT) (Anisimova and Gascuel 2006). Additionally, we estimated gene trees for each locus using IQ-TREE, collapsed all nodes with less than 80% SH support, and then inferred a

coalescent-based phylogeny with ASTRAL v.5.7.8 (Zhang *et al.* 2018). These two approaches returned similar topologies (Supporting Information Fig. S2), so we focused all subsequent analysis on our concatenated tree.

Then, based on the phylogenomic backbone and previously published phylogenies (Singhal *et al.* 2017a, 2018a), we split the tree into 32 clades of approximately the same phylogenetic depth (Supporting Information Fig. S3). For each clade, we generated a concatenated alignment across target-capture, mtDNA, and ddRAD data of all ingroup samples and three outgroups. For our target-capture data, we only used the 25 most clock-like loci as identified by SortaDate (Smith *et al.* 2018); using all ~5000 loci drowned the signal from both the ddRAD and mtDNA data. For ddRAD data, we only included those sites that were 60% complete across sampled individuals (number of sites ranged from 159 to 943 kb). We then inferred the clade phylogeny, constraining the topology to the phylogenomic backbone and partitioning the alignment by marker type (mtDNA, ddRAD, target capture) and site type (codon position for mtDNA). We used PartitionFinder to automatically select the best-fitting partition and sequence evolution model (Lanfear *et al.* 2012). We measured nodal support using both ultrafast bootstraps and SH-aLRT. Finally, using the R package ape v.5.8 (Paradis *et al.* 2004), we grafted these 32 clade-level trees into our phylogenomic backbone. Before grafting the tree, we scaled branch lengths in the clade-level tree by comparing correlations between branch lengths in the target-capture, phylogenomic backbone tree and clade-level trees (Fig. S4). To do so, we identified individuals that were sampled across both trees—including outgroups—and used a linear model to estimate the slope describing the relation of branch lengths in the target-capture versus clade-level tree. Average slope was 1.22 (95% range: 0.99–2.23).

We then dated the synthetic tree using TreePL v.1.0 (Smith and O’Meara 2012). For our constraints, we used the same three secondary constraints used in Rabosky *et al.* (2014a), which spans the age of the Australian sphenomorphine radiation, the Sahulian sphenomorphine radiation, and all sphenomorphines (Supporting Information Fig. S5). We used the random sampled cross-validation to identify the best smoothing parameter (*smooth* = 0.1).

Defining provisional taxonomic frameworks

We tested the effects of four different taxonomic frameworks on our inference of diversification patterns (Table 2; Fig. 1). The first framework, ‘morphological’, was restricted to species that have been described using only morphological data. Because most currently recognized sphenomorphine species have been described based on morphological attributes, this listing is nearly synonymous with the ‘official list of Australian species’ maintained by the Australian Society of Herpetologists (Australian Society of Herpetologists 2023), which in turn is mirrored by an all-encompassing reptile species list (Reptile Database; Uetz *et al.* 2021). Nevertheless, we conducted an extensive review of the literature to identify which sphenomorphine species were diagnosed partially or completely also based on genetic data, which corresponds to only 28 currently recognized species (~10% of currently recognized diversity; Supporting Information Table S2). To ‘reconstruct’ our knowledge of sphenomorphine

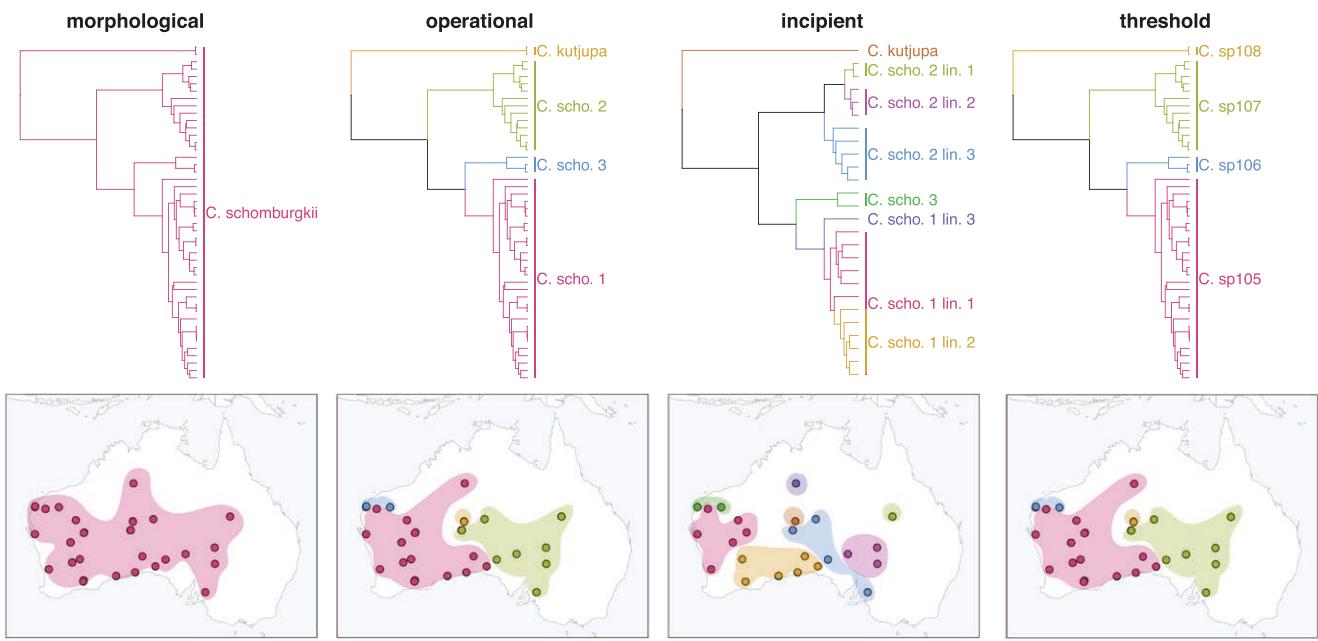


Figure 1. An example from one morphologically defined species (*Ctenotus schomburgkii*) showing how species boundaries differed across our four taxonomic frameworks: morphological, operational, incipient, and threshold. Note that the incipient delimitation spans fewer individuals as it could only be implemented on individuals for which we collected population genomic data.

taxonomy based exclusively on morphology, we ‘synonymized’ or ‘re-elevated’ those species whose recognition has been recently altered based on genetic analyses. Ultimately, this taxonomy of morphological species reflects decades-long taxonomy practices undertaken by relatively few specialists based on a consistent set of traits.

We derived a second framework, ‘operational’, to represent our current best understanding of species limits in sphenomorphines as informed by both morphological and genetic data. As is true of many species with low dispersal, previous range-wide DNA sequencing of sphenomorphines has revealed that many morphologically defined species contain multiple, divergent cryptic lineages (Aplin and Adams 1998, Hutchinson et al. 2006). During the past decade, we have characterized these lineages to define an operational taxonomic framework for this clade (Rabosky et al. 2014b, 2017, Singhal et al. 2017a, 2018a, 2022, Prates et al. 2022a, b, 2023, 2024, Farquhar et al. 2024). Many putative operational species in this clade were delimited through genetic clustering and phylogenetic approaches, although many of the genetically defined units were consistent with the traditional (morphological) taxonomy. These provisional species were then refined through a diversity of techniques, including identifying breaks in isolation-by-distance patterns across geographical space, comparing patterns of genetic and morphological variation to identify discontinuities, and characterizing patterns of admixture at parapatric boundaries between putative taxa. Thus, this operational species framework uses extensive sampling to unite across geographical, genetic, and morphological data, and it helps us address the role of unrecognized diversity in creating taxon murk. Here, we additionally categorized the relationship of each operational species to its most similar morphological species. Operational species were either categorized as ‘identical’

to a morphological species, ‘split’ indicating that it consisted of a morphological species being split into two or more units, or ‘combined’ indicating that it consisted of multiple morphological species collapsed into one operational species.

Third, we applied clustering approaches to the ddRAD genomic dataset to delimit an ‘incipient’ taxonomic framework, further splitting our operational species into a series of population-level lineages that might represent incipient species. If given enough time, these incipient species could emerge into what we recognize as ‘good’ species (Dynesius and Jansson 2014, Etienne et al. 2014). This taxonomic framework allows us to consider the effects of taxon murk due to protracted speciation. For this taxonomy, we only considered operational species for which we sampled three or more individuals for ddRAD data ($N = 123$; 49% of species). For these species, we used VCFtools v.0.1.17 (Danecek et al. 2011) to filter the variant datasets generated per species to only include sites with a minimum depth of 5, a minor allele count of 2, and a maximum of 30% missing data, and to thin sites to one random site per 100 bp. We then used fastStructure v.1.0 (Raj et al. 2014) to estimate the most likely number of genetic populations (K) and their identities. We ran fastStructure from $K = 1$ to the maximum number of individuals sampled of each species, and we used the ‘model components’ method to choose the best K . Choosing the best K is nontrivial (Evanno et al. 2005), so we consider this analysis solely descriptive. We visually inspected the phylogenetic and geographical distribution of these genetic populations, finding that most populations are monophyletic and geographically circumscribed (Supporting Information Fig. S6). These genetic populations are our incipient species.

Our final ‘threshold’ framework delimited species-level taxa using a quantitative threshold (τ ; a ‘veil line’) for species-level

divergences, below which all younger divergences would be collapsed to a single species-level lineage. Thus, a value of $\tau = 1$ Myr would result in a phylogeny where all divergences that occurred less than 1 Myr before the present would be collapsed into a single ‘threshold species’ for subsequent analysis (Fujisawa and Barraclough 2013). Note that this approach collapses divergences regardless of whether any particular taxonomic scheme recognizes them as inter- or intraspecific, and is thus solely dependent on phylogenetic branching times. While branch lengths can vary due to the impacts of organismal traits on molecular evolution (Ivan *et al.* 2021), this framework should be largely free from subjective taxonomic bias. As such, this taxonomic framework allows us to consider the effects of taxon murk due to differences in taxonomic practice and evolutionary dynamics of taxonomically relevant characters across clades. We tested a range of τ values from 0.1 to 10 Myr and present in the main text results from a τ value of 2.5 Myr.

We regard our operational, incipient, and threshold delimitations as provisional. They are delimitation hypotheses that need more exploration before they can become formal, revised taxonomic treatments. In particular, we acknowledge that the population-level lineages in our incipient delimitation might not persist long enough to become ‘good’ species and that genetic divergence is just one metric by which incipient species can be identified.

Analyses

Comparing across taxonomic frameworks

Each taxonomic framework used different criteria to delimit species-level taxa, and, thus, we might expect these units to be qualitatively different across frameworks. We explored differences across these units in two ways. First, we defined divergence time to their nearest sister species using the individual-level phylogeny. Second, using a ddRAD variant dataset filtered only for depth (depth $> 5x$) and missingness (missingness $< 50\%$), we calculated F_{ST} between species (Reich *et al.* 2009). For these analyses, we compared a taxon to its closest relative; in cases where a taxon was equally related to multiple taxa, we included all comparisons. For comparisons involving incipient species, we only compared incipient species to other incipient species.

Characterizing diversification patterns

For each of our four taxonomic frameworks (Table 2), we subsampled our all-individual phylogeny to create lineage-level phylogenies that reflect the diversity of each of these delimitations. In the rare case where the samples assigned to a species were nonmonophyletic, we included the sample from the largest monophyletic group as our representative tip.

We then used these phylogenies to estimate tip speciation rates with three methods: the DR statistic (Redding and Mooers 2006, Jetz *et al.* 2012), BAMM v.2.5.0 (Rabosky 2014), and CLaDS (Maliet *et al.* 2019, Maliet and Morlon 2022). The DR statistic is a semiparametric approach that estimates ‘tip’ speciation rates as the weighted mean of the inverse of branch lengths (Title and Rabosky 2019). BAMM and CLaDS use a Markov chain Monte Carlo (MCMC) approach to simulate posterior distributions of diversification model parameters. CLaDS assumes that speciation rates change discretely on every branch

of the phylogeny and potentially allows tracking of fine-grained rate variation—but the method will also infer rate variation when none is present, because all branches are assumed to have unique rate parameters. On the other hand, BAMM only infers new rate parameters when there is sufficient signal in the data to favour a distinct rate regime; the approach is conservative but also robust to inferring spurious rate variation. Thus, these two methods provide complementary approaches to infer tip speciation rates, and in practice, they have been found to provide broadly congruent inferences (Vasconcelos *et al.* 2022). We ran BAMM for 1e8 MCMC generations for triplicate runs for each phylogeny. Priors were calculated using the setBAMMpriors function in BAMMtools v.2.1.11 (Rabosky *et al.* 2014c); we left all other run parameters as default. We assessed convergence by visually inspecting the log-likelihood MCMC trace, calculating effective sample sizes using coda v.0.19-4.1 (Plummer *et al.* 2006), and comparing tip speciation rates across runs. For CLaDS, we ran each phylogeny under three separate runs, stopping the MCMC chain automatically when the Gelman convergence statistic dropped below 1.05. For both methods, we accounted for unsampled tips by providing sampling fractions at the genus level. To assess differences in tree-wide diversification rates and in support for topological rate shift configurations, we compared the credible shift sets for each taxonomic scheme (Rabosky *et al.* 2014c).

To determine if speciation rates have slowed down through time, we first visually evaluated estimates of speciation rate through time using BAMMtools. Then, we calculated the gamma (γ) statistic on the phylogeny using gammaStat implemented in ape. The γ statistic is a relatively simple yet robust index of the extent to which speciation times are concentrated early in the history of a clade, relative to the expectation under a constant-rate pure birth diversification process (Pybus and Harvey 2000). However, if a tree has only been partially sampled—particularly if the missing tips are relatively young— γ can be artefactually negative leading to mistaken inference of a slowdown. Accordingly, we conducted two sets of simulations to test the effects of these potential biases. In the first set of simulations, we tested how partial sampling might impact our inference of a slowdown. To do so, we simulated trees under a pure birth process. We then subsampled anywhere from 10% to 100% of the tips to result in a total of 251 sampled tips, the same number of species in our operational framework. We either subsampled tips randomly or with weak or strong bias, such that the unsampled tips were either slightly younger or much younger than sampled tips. For weak bias, unsampled tips were all in the youngest 50% of species ages; for strong bias, unsampled tips were in the youngest 25%. This approach might provide a good model of taxonomic practice whereby researchers are more likely to recognize deeper divergences, but where recent divergences—perhaps due to fewer accumulated phenotypic differences between putative species—would be less likely to be recognized as good species. We then calculated γ for each simulated, subsampled tree.

In the second set of simulations, we tested how failing to include species arising from protracted speciation might affect our ability to accurately infer a slowdown. Here, we added anywhere from 20 to 500 incipient species to our operational species phylogeny. To reflect

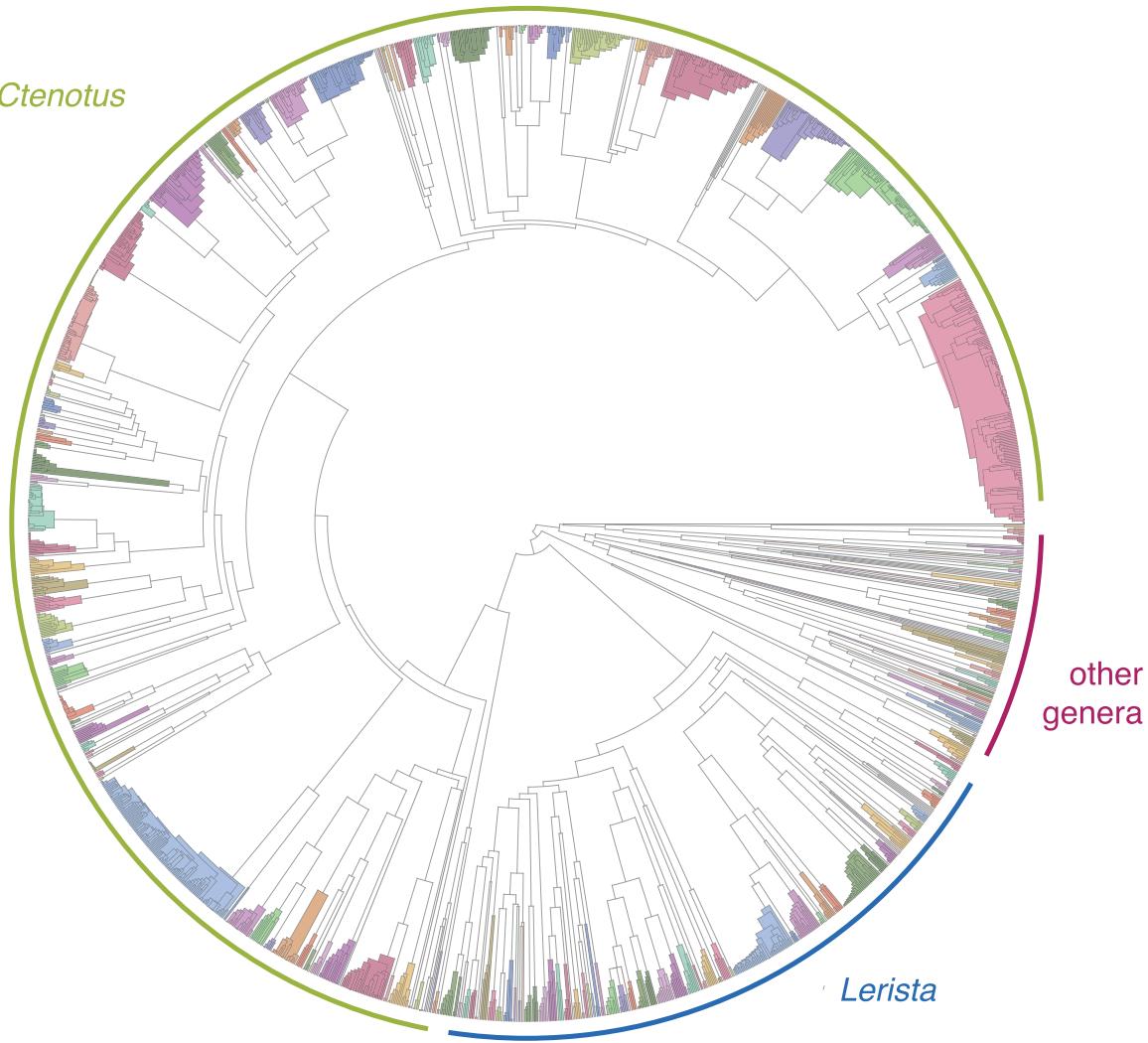


Figure 2. Phylogeny of the sphenomorphine clade, spanning 1941 individuals across 200 morphological species and 251 operational species. The two most species-rich genera in the sphenomorphines are labelled (*Ctenotus* and *Lerista*); the paraphyletic grouping of ‘other genera’ consists of 17 genera. Colours demarcate operational species.

their incipient status, we capped the maximum age of these species as the median splitting time of our operational taxon. We then used a pure birth process to generate a distribution of ages for these lineages via corsim in the TreeSim v.2.4 package and used bind.tip in phytools v.2.1-1 to randomly bind these new lineages to our phylogeny (Stadler 2011, Revell 2024). We then calculated γ for each tree.

Data analysis and visualization

All data were analysed and processed using Python v.3.10.10 and R v.4.2.1. Scripts are available at <https://github.com/singhal-sphenophylo>. Data were summarized and visualized using the R packages ape v.5.8, cowplot v.1.1.3, dplyr v.1.1.4, ggplot v.3.5.1, and tidyverse v.1.3.1 (Paradis et al. 2004, Wickham 2016, Wilke 2016, Wickham et al. 2019).

RESULTS

Data collection

This study presents target-capture (AHE and SqCL) data newly collected for 233 individuals; these data had low missingness and

high quality for all individuals (Supporting Information Fig. S7). On average, we recovered 96.0% of the targeted loci. Combined with our previously published target-capture data, we were able to infer a phylogenomic backbone for 296 individuals based on 5277 loci (Fig. S2).

Phylogenetic inference

Our phylogenetic inference resulted in a final, ultrametric tree of 1941 tips (Fig. 2). Nodal support was typically high across deeper phylogenetic nodes and decreased towards the present (Supporting Information Fig. S8). As has been noted in other studies (Sistrom et al. 2013, Singhal et al. 2018b, Zozaya et al. 2019), many sphenomorphine morphological species consist of multiple, deeply structured lineages, some of which are paraphyletic. In contrast, our operational species were mostly monophyletic. A few operational species contained individuals that were initially assigned to one taxon based on morphology and geography but then belonged to another taxon’s clade. We examined these manually; most of these are examples of misidentification, which is common in field-based surveys of morphologically conservative complexes.

The species-level topologies largely matched previously inferred phylogenies based on smaller, mitochondrial-driven datasets (Skinner *et al.* 2013, Rabosky *et al.* 2014a). The most notable exception was the placement of *Notoscincus*, which in previous phylogenies was inferred to be sister to all Australian sphenomorphines (Supporting Information Fig. S9). The age of all sphenomorphines was inferred as 20.3 Mya, compared to 25.3 Mya in Skinner *et al.* (2013) and 24.2 Mya in Rabosky *et al.* (2014a) and the age of the *Ctenotus* and *Lerista* split was inferred as 19.5 Mya compared to 21.2 Mya in Rabosky *et al.* (2014a). Thus, our phylogeny inferred a shorter interval between the crown age of all Australian sphenomorphines and the ancestry of *Ctenotus* and *Lerista* relative to previous phylogenies.

Analyses

Comparing across taxonomic frameworks

We categorized our sampled individuals across four provisional delimitation approaches (Table 2). Our ‘morphological’ taxonomic delimitation sampled 200 morphological species, whereas our ‘operational’ delimitation sampled 251 operational species. Of these operational species, 132 were identical to morphological species, 108 were split from morphological species, and 11 were combined across multiple morphological species (Fig. 3). For the 123 operational species for which we sampled three or more individuals, we inferred an average of 2.1 genetic clusters (range: 1–4 clusters). Our ‘incipient’ delimitation thus sampled 402 species overall, of which 151 were incipient species. Finally, our ‘threshold’ delimitation (as defined by $\tau = 2.5$ Myr) sampled 258 threshold species, 87% of which were identical to an operational species (Supporting Information Fig. S10).

We compared patterns of divergence (F_{ST} , divergence time) across species-level taxa delimited by each taxonomic framework to understand differences among these units. Because patterns of divergence overlapped significantly among the morphological, threshold, and operational taxonomies (Supporting Information Fig. S11), we focus here on comparing traditionally defined morphological species to putatively cryptic operational species and incipient species. We find that, while newly split, putatively cryptic species are slightly younger than morphological species (Fig. 4B), distributions of divergence times and F_{ST} levels are mostly overlapping for these groups (Fig. 4B; Fig. S11). In contrast, distributions of divergence times and F_{ST} levels are discontinuous between incipient and operational species. The lineage accumulation curve for all sampled individuals exhibits a clear inflection point around ~2 Mya; nearly all within-incipient species coalescences occur near or after that inflection point (Fig. 4A). Incipient species are younger (Fig. 4B) and less genetically divergent (as measured by F_{ST} ; Fig. S11B) than other species; we see a threshold around F_{ST} of 0.6 that seems to divide incipient and nonincipient species.

Characterizing diversification patterns

We then conducted analyses to determine how taxon murk affects our understanding of diversification dynamics. Our operational, threshold, and incipient delimitations capture 51, 58, and 202 more taxa respectively than the morphological delimitation. The lineage accumulation curves for the operational and threshold species depart from the corresponding accumulation

trajectory for the morphological species about 5 Mya, and the lineage accumulation curve for the incipient species diverges from that observed for operational species about 2 Mya. Further, the incipient delimitation—unlike the morphological and operational delimitation—shows no evidence of a plateau in lineage accumulation towards the present (Fig. 5A).

Despite these differences, overall diversification dynamics are similar across all four taxonomic frameworks. Across all four frameworks, BAMM inferred a doubling of speciation rate at the ancestor of *Ctenotus* and *Lerista* (Fig. 5; Supporting Information Fig. S12). While speciation rates are similar across the operational and morphological taxonomies, speciation rates are overall higher in the phylogeny including incipient species (Fig. 5F), although this is perhaps expected given the substantial increase in the number of included tips. These results are also robust across inference methods; both CLaDS and the DR statistic also show a doubling in rates in *Ctenotus* and *Lerista* relative to other genera (Fig. S13).

We then tested for a slowdown in diversification rates across the sphenomorphine phylogeny. Our posterior rate reconstructions (BAMM) reveal a clear pattern of rate deceleration across *Ctenotus*, *Lerista*, and the other genera in the radiation (Supporting Information Fig. S14). We then estimated gamma (γ) from the time-calibrated phylogeny under each taxonomic scheme (Table 2), finding highly negative estimates for each taxonomic framework (γ for the operational taxonomy = -10.7; Table 2; Fig. 6). Because γ can be artificially negative if sampling is incomplete or biased towards older lineages, we conducted two simulations to test the robustness of this result. In the first set of simulations, we found that the true diversity of sphenomorphines would need to be on the order of 1200 species (versus 270 currently recognized) to generate a γ as negative as the observed empirical value (Fig. 6). If sampling is strongly biased towards older divergences, such that unsampled species represent the youngest divergences in the phylogeny, the true diversity of sphenomorphines would need to be on the order of 500 species to generate a γ as negative as the observed empirical value. In the second analysis, we simulated the addition of incipient lineages ($N = 20$ –500) to our operational species phylogeny and then calculated γ . Even a large increase in the number of incipient lineages ($N \sim 100$ species or 30% of total diversity) still resulted in a highly negative γ value (mean $\gamma = -6.1$). Only when we added a substantial number of incipient lineages ($N \sim 300$ lineages or >50% of total diversity) did we see γ approach zero (Fig. S15).

DISCUSSION

Species-level phylogenies are essential for many comparative and macroevolutionary analyses. However, the birth–death model that is typically used to conceptualize (and analyse) the diversification process ultimately assumes that we have accurately delimited—or accounted for, through a sampling model—the tip-level units that undergo speciation and extinction. Yet, the tips in our empirical phylogenies might fail to meet these assumptions because of the uncertainty associated with the sampling of tips and even the nature of tips themselves, a phenomenon we refer to as taxon murk (Table 1). Taxon murk

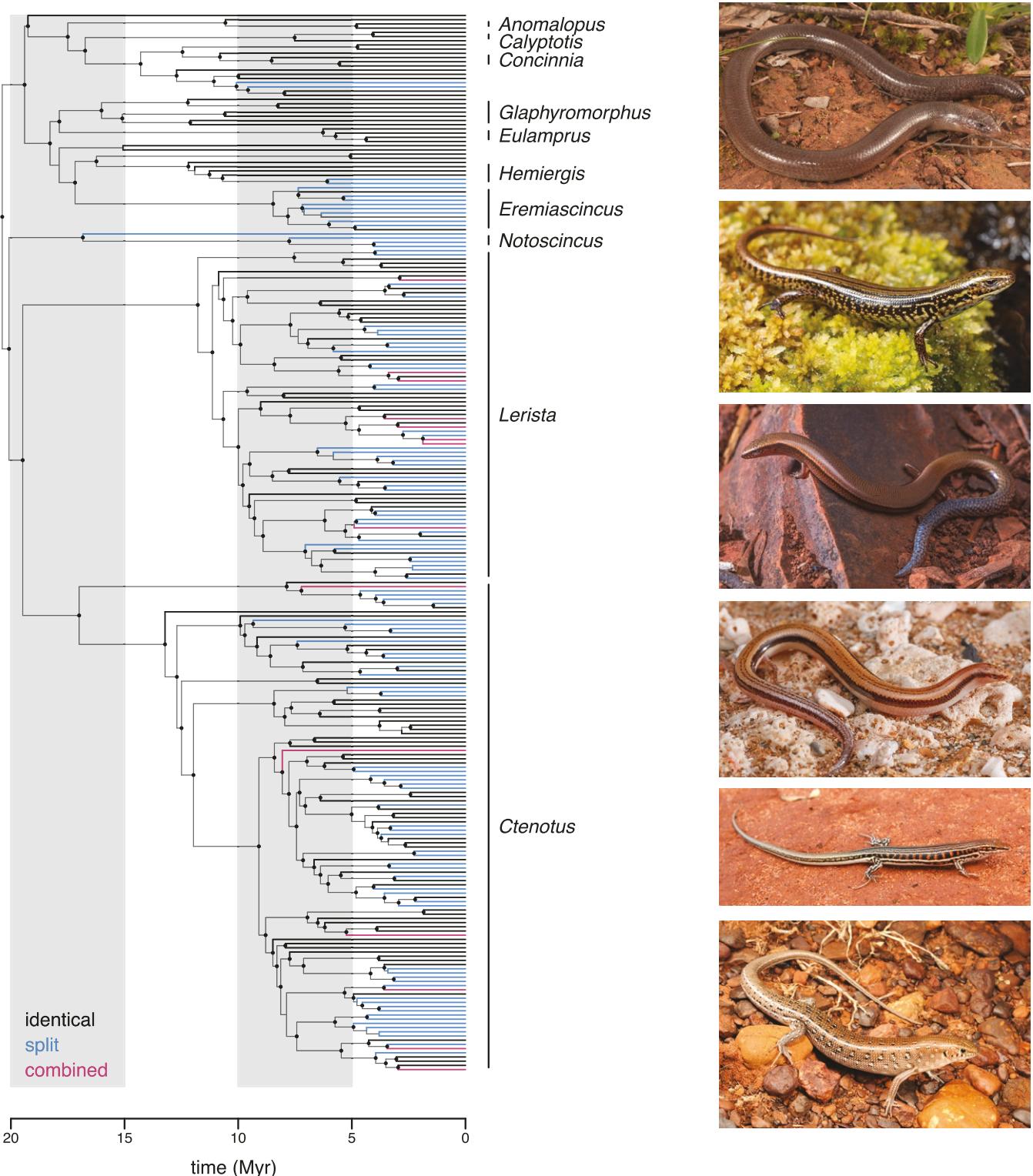


Figure 3. Phylogeny of species as defined by our operational taxonomic framework. We randomly subsampled one individual per operational taxon from our full phylogeny shown in Figure 2. Black points at nodes indicate branches with >95 support as measured by Shimodaira–Hasegawa approximate likelihood ratio tests. Genera with three or more sampled species are labelled. Terminal branches coloured blue are taxa that are split relative to a morphological species, magenta terminal branches combine across two or more morphological species, and black terminal branches are identical to a morphological species. Split taxa are relatively common in this phylogeny, and most diverged around ~5 Mya. From top to bottom, images are of *Anomalopus leuckartii* (J. Farquhar), *Eulamprus kosciuskoi* (J. Farquhar), *Lerista chalybura* (J. Farquhar), *L. bipes* (J. Farquhar), *Ctenotus schomburgkii* (D.L.R.), and *C. pantherinus* (E. Vanderduys).

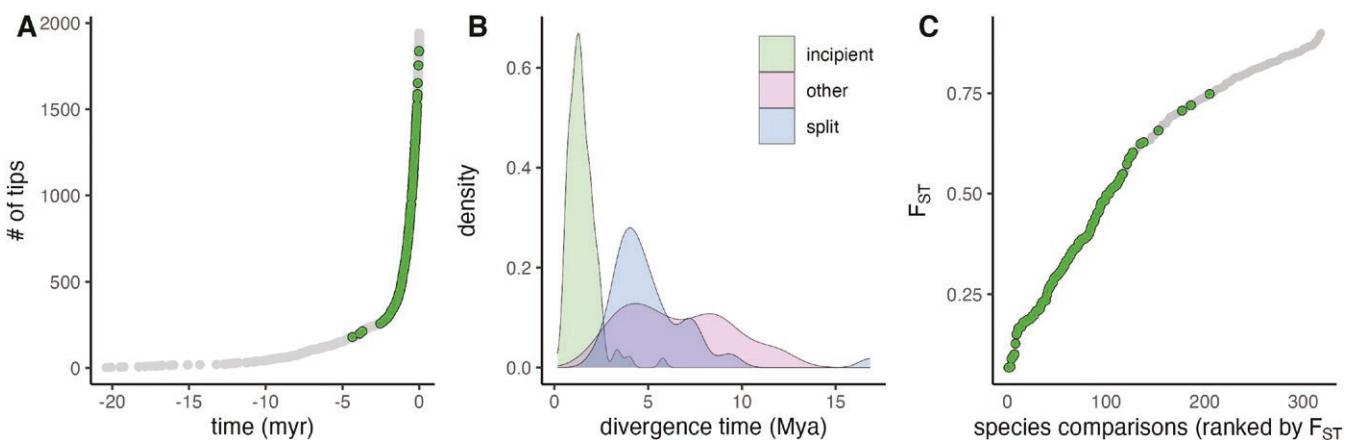


Figure 4. Patterns of divergence between incipient and operational species. Comparisons between operational species are further divided into those between newly recognized splits within morphological species ('split') and all other comparisons ('other'). A, a lineage-through-time plot of all sampled individuals (shown in grey) shows the crown ages for the incipient species all fall near the inflection point (or later) in the lineage accumulation curve. B, 'Split' species are younger than other species comparisons on average, but divergence times are completely overlapping. C, there is a break in extent of F_{ST} between incipient species comparisons and all other comparisons (shown in grey).

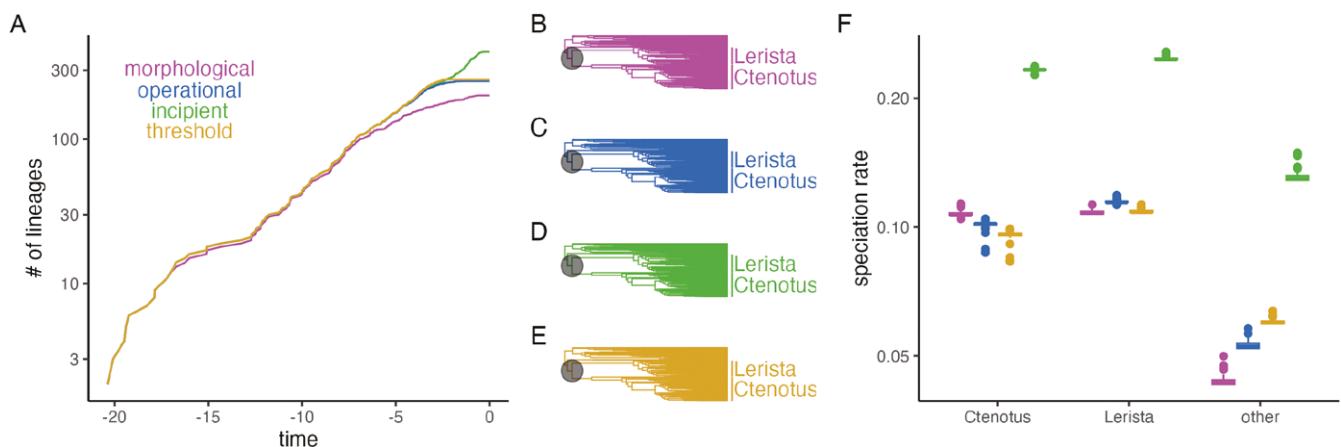


Figure 5. The effects of taxonomic framework on inference of speciation rates. A, lineage-through-time plot for the four taxonomies. B–E, inference of rate shift (as inferred by BAMM) for (B) morphological, (C) operational, (D) incipient, and (E) threshold taxonomic delimitation. F, speciation rates (as inferred by BAMM). Despite differences in lineage accumulation patterns towards the present, all four taxonomies show an approximately doubling in speciation rate at the base of the *Ctenotus* and *Lerista* clades.

can systematically mislead inference of diversification patterns, including the causes of global biodiversity gradients (Freeman and Pennell 2021) and the prevalence of so-called 'early burst' speciation (Etienne and Rosindell 2012). Yet, few studies have assessed the impact of taxon murk (Frates et al. 2024), potentially because addressing some potential sources of tip unit uncertainty requires extensive intraspecific data. Here, we tested whether and how taxon murk affects qualitative and quantitative inferences about the dynamics of speciation through time and among clades, by using dense population-level sampling of a diverse clade of Australian lizards.

Taxon murk in the Australian sphenomorphines

The so-called 'Linnean shortfall' (Hortal et al. 2015)—the discrepancy between true numbers of species and those we currently recognize—might pertain to groups that are assumed to be reasonably well known, such as terrestrial vertebrates (Freeman and Pennell 2021, Melville et al. 2021, Flanagan et al.

2024). Groups or geographical regions that have received less taxonomic attention might be especially likely to harbour substantial cryptic or otherwise unrecognized biological diversity, which could significantly impact our understanding of diversification in these groups and regions. A priori, we would expect that the Australian sphenomorphine radiation should be especially impacted by heterogeneity in taxonomic practice: it is a diverse clade that, on a per-species basis, has received far less taxonomic attention than many comparable clades. Indeed, a substantial fraction of recognized sphenomorphine species are the result of work from a single taxonomist and have not been scrutinized with population genetic data (Prates et al. 2024).

However, our results suggest that sphenomorphines are only characterized by a modest Linnean shortfall. The operational taxonomy we considered has a (provisional) increase in 51 species relative to the number of sampled morphological species, most of which result from splitting morphological species into multiple, putatively cryptic species (Fig. 1). We contend that

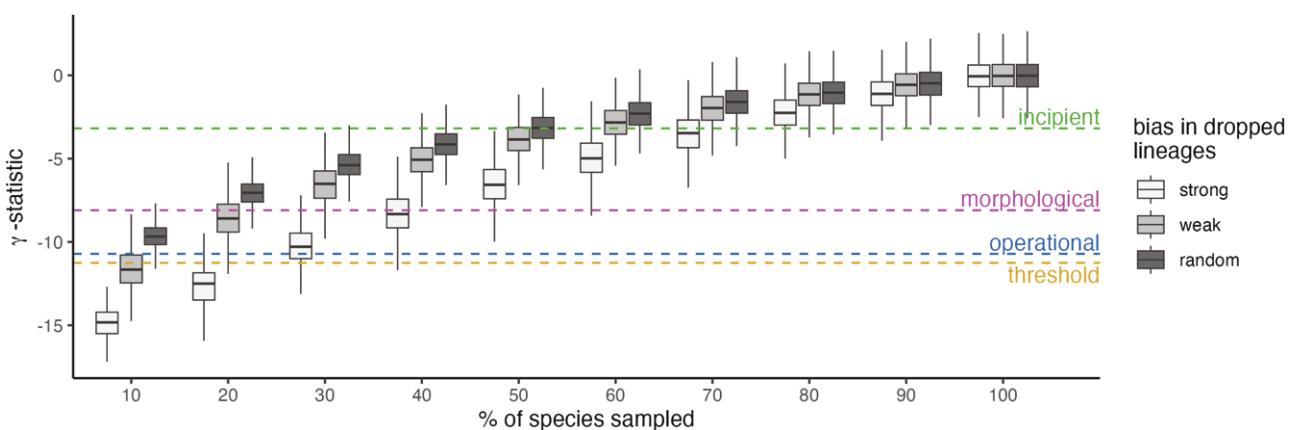


Figure 6. The effects of taxon murk on the inference of a slowdown in diversification rates, as measured by the gamma (γ) statistic. Negative γ values indicate a slowdown in rates. Horizontal lines reflect the γ values estimated from the empirical phylogenies for the four taxonomic frameworks. Boxplots indicate the distribution of γ values for phylogenies simulated under a pure birth model. To simulate the effects of missing data, phylogenies were subsampled to represent 251 tips, or the number of species in our operational framework. Tips were subsampled either randomly or with weak or strong bias, such that the unsampled tips were either slightly younger or much younger than sampled tips. Our estimated level of sampling for the operational framework is 76%. These results suggest our highly negative γ is unlikely to be due to incomplete sampling, because only extreme levels of undersampling would lead to a false positive.

many of these operational species are candidates for full species status; we note that they exhibit similar levels of temporal isolation as morphologically defined taxa (Fig. 4B; blue versus magenta). We contrast these operational species to the incipient species, which we defined as the genetic populations identified through clustering algorithms (fastStructure; Raj *et al.* 2014). We expect that many of these incipient species will fail to persist over longer timescales (Rosenblum *et al.* 2012, Dynesius and Jansson 2014, Harvey *et al.* 2019), and we would need greater evidence for their genetic, reproductive, and ecological distinctiveness, including sampling in areas of geographical proximity (Singhal *et al.* 2018b, Burbrink *et al.* 2021, Chambers *et al.* 2023), before they could be ascribed species status.

While our operational taxonomic framework identified ~50 more species than our morphological framework, this potential increase in species diversity is necessarily an underestimate, as many species remained poorly sampled in our genomic dataset. Approximately 110 currently recognized Australian sphenomorphine taxa are either not included in our dataset or are represented by just one sample, and thus, we could not evaluate if these taxa contained unrecognized diversity. However, these taxa are mostly small-ranged and geographically restricted forms, whereas most of the newly split operational and incipient species entail the geographical partitioning of taxa with moderate to large geographical ranges (see Fig. 1 as an example). As such, we expect that these undersampled taxa are considerably less likely to harbour cryptic diversity than the better-sampled, wide-ranging taxa in our dataset.

Still, we can estimate the probable true number of species in the sphenomorphines by making some simplifying assumptions. Divergence patterns across taxonomic schema revealed a clear inflection point for divergences <2 Myr; nearly all incipient species are younger than this threshold (Fig. 4B). Applying a 2-Myr yardstick for recognizing phylogroups as distinct species, as through our thresholding scheme, we would recognize 299 species (Supporting Information Fig. S16A), or a 49% increase in

species-level diversity relative to the morphological taxonomy. This delimitation makes the (strong) assumption that 2 Myr of separation is generally associated with the evolution (or completion) of strong reproductive isolation between allopatric lineages as inferred based on an inflection point in the relationship between F_{ST} and time (Fig. S17). Given these caveats, we predict that the true number of evolutionarily distinct and reproductively isolated lineages—‘good species’—within the Australian sphenomorphine radiation is on the order of 320–370 species, versus nearly 280 currently recognized species (Uetz *et al.* 2021, Australian Society of Herpetologists 2023).

Diversification inference in sphenomorphines is largely robust to taxon murk

Sampling phenomena that contribute to taxon murk (Table 1) are recognized by many researchers as a possible explanation for spurious diversification slowdowns (Pybus and Harvey 2000, Cusimano and Renner 2010, Etienne and Rosindell 2012, Moen and Morlon 2014). For example, both cryptic species diversity and the presumably protracted nature of the speciation process can result in underestimates of the true species diversity in a clade (Bickford *et al.* 2007, Etienne and Rosindell 2012). This undersampling can then lead us to infer apparent slowdowns in speciation rate when rates have remained constant—or even increased—through time.

Our results suggest that general qualitative and quantitative features of speciation in sphenomorphines are largely robust to taxon murk. Regardless of taxonomic scheme (Table 2), our results recover two basic features of sphenomorphine diversification that have been reported in previous studies (Rabosky *et al.* 2007b, 2014a): first, the speciose genera *Ctenotus* and *Lerista* have speciation rates approximately twice as fast as the other sphenomorphine genera; and second, speciation rates in the clade as a whole have undergone a pronounced deceleration through time. We find it especially remarkable that speciation rates estimated under the ‘incipient’ scheme preserve both

this relative rate difference (Fig. 5F) as well as the similarity in rates between *Ctenotus* and *Lerista*, because there are numerous ecological and biogeographical differences between clades. For example, *Ctenotus* species are surface active, fully limbed taxa, whereas *Lerista* species tend to be limb-reduced burrowers; these differences in morphology are mirrored in patterns of spatial genetic structure (Singhal *et al.* 2018a). Still, we find no evidence for markedly faster ‘incipient’ speciation in *Lerista* relative to *Ctenotus* (Fig. 5F, green).

While numerous studies have reported apparent speciation slowdowns from phylogenetic data (Rüber and Zardoya 2005, Kozak *et al.* 2006, McKenna and Farrell 2006, McPeek 2008, Phillimore and Price 2008), few have rigorously assessed the potential contribution of taxon murk to the pattern, as we have done. We find that the overall slowdown in speciation rates reported previously at the base of the sphenomorphine radiation appears remarkably robust to taxonomic scheme. The gamma (γ) statistic values for the morphological, operational, and threshold approaches are extremely unlikely under a constant-rate diversification process, even with relatively extreme taxonomic undersampling (Fig. 6). Our intraspecific genomic sampling does not reveal any evidence that sphenomorphine speciation rate slowdowns are the result of an extensive but unsampled reservoir of cryptic diversity; many hundreds of such unknown species would be required to account for a slowdown effect similar to what we observe (Supporting Information Fig. S15). We also found that, when using the threshold approach, we recovered both a doubling of speciation rates and a slowdown across age thresholds from ~2 to 7.5 Myr (Fig. S16), suggesting that our key diversification inferences are robust across a broad range of delimitation schema.

To what extent can these results be generalized to numerous other studies that have reported temporal slowdowns in speciation rates? Clearly, the impact of taxon murk will be a function of clade-specific sampling uncertainties, and we thus consider it unlikely that any simple significance threshold will hold across different taxonomic groups. Nonetheless, to determine whether any ‘rules of thumb’ might help researchers gauge the potential for spurious results due to taxon murk, we compiled and/or estimated γ values for a set of diverse clades—some previously published (Supporting Information Table S3), and others computed from a recent time-calibrated phylogeny of squamate reptiles (Title *et al.* 2024). We then assessed whether those values would be significant under both the traditional approach for determining significance thresholds with γ (Pybus and Harvey 2000) as well as under a modified scheme that allowed for additional unsampled diversity plus a bias in favour of sampling deeper lineages (Fig. 6).

Our results (Fig. 7) suggest that, in general, low to moderate levels of taxon murk would affect the significance of some γ estimates. Our results suggest that phylogenies with ‘barely’ to moderate significance—e.g. $\gamma > -5$ —are susceptible to taxon murk. In particular, some apparent early burst patterns could be nonsignificant (Fig. 7: grey circles) given some relatively minor assumptions about levels of cryptic diversity and the extent to which missing species are a phylogenetically random sample. On the other hand, phylogenies with $\gamma < -5$ are generally inconsistent with constant-rate speciation, even with

relatively high percentages of missing taxa (Fig. 7: black circles). Regardless, one of the most striking features of Figure 7 is the extent to which results for the Australian sphenomorphines deviate from patterns in other clades, including other squamate reptiles (Fig. 7B).

Tree construction biases and early burst patterns

Beyond taxon murk, underparameterized models of sequence evolution can also lead to spurious early burst patterns. These models can underestimate the numbers of changes along early branches during a radiation (Revell *et al.* 2005), thus resulting in time-calibrated trees with disproportionately shorter branches near the base that yield (apparent) early burst patterns of lineage diversification. Because the models we use to approximate the sequence evolutionary process are never as complex as reality, we suspect that even complex models of sequence evolution are unable to fully eliminate this effect. This hypothesis (tree construction artefact) predicts that we should observe a ‘compression’ effect, such that branch lengths should be systematically and progressively more underestimated closer to the root of a phylogeny. Under this model, as we sample older and more inclusive clades, we would be including branches with greater bias in our analysis. This in turn would lead to even greater evidence of a slowdown on older nodes that span nonsphenomorphine taxa. In contrast, if the slowdown (or speciation burst) is associated with a particular biogeographical event, such as the colonization of Australia by a sphenomorphine ancestor, we would not expect to see continued evidence for slowdown (e.g. shorter branches) upon inspection of the ancestral branches subtending the focal clade.

The dataset we generated for the present study does not include non-Australian representatives, but the time-calibrated squamate phylogeny from another recent study (Title *et al.* 2024) includes dense sampling of sphenomorphine taxa more generally (227 species). We extracted internal branch lengths for the three immediate (rootwards) ancestral branches leading to the Australian sphenomorphine radiation and compared them to the branch lengths observed for the earliest internal branches within the Australian subgroup, all from the same phylogenetic framework (Title *et al.* 2024). These comparisons suggest that tree construction biases are unlikely to be the primary cause of the slowdown effect. All three branches ancestral to the Australian clade are markedly longer (11.1, 4.0, and 5.1 Myr) than the first five internal branches within the Australian clade (0.7, 0.8, 1.3, 1.6, and 2 Myr). Under a tree construction bias scenario, we might expect these more ancestral branches to be similar in length to, or shorter than, the earliest branches in our focal clade. Instead, we find that the shortest branches are coincident with the clade’s radiation in Australia. In addition, if compression was affecting branch length estimates, more inclusive sampling of deeper branches should strengthen the signal of an overall slowdown effect. However, we see the opposite pattern: the estimated γ for the Australian sphenomorphine radiation using the Title *et al.* phylogeny is -11.1 (compared with $\gamma = -10.7$ for this study; Fig. 6), whereas gamma for the Sphenomorphinae as a whole (with 65% species sampled) is -7.5 . Collectively, these observations suggest that the early burst signal in Australian sphenomorphines is robust to tree construction biases.

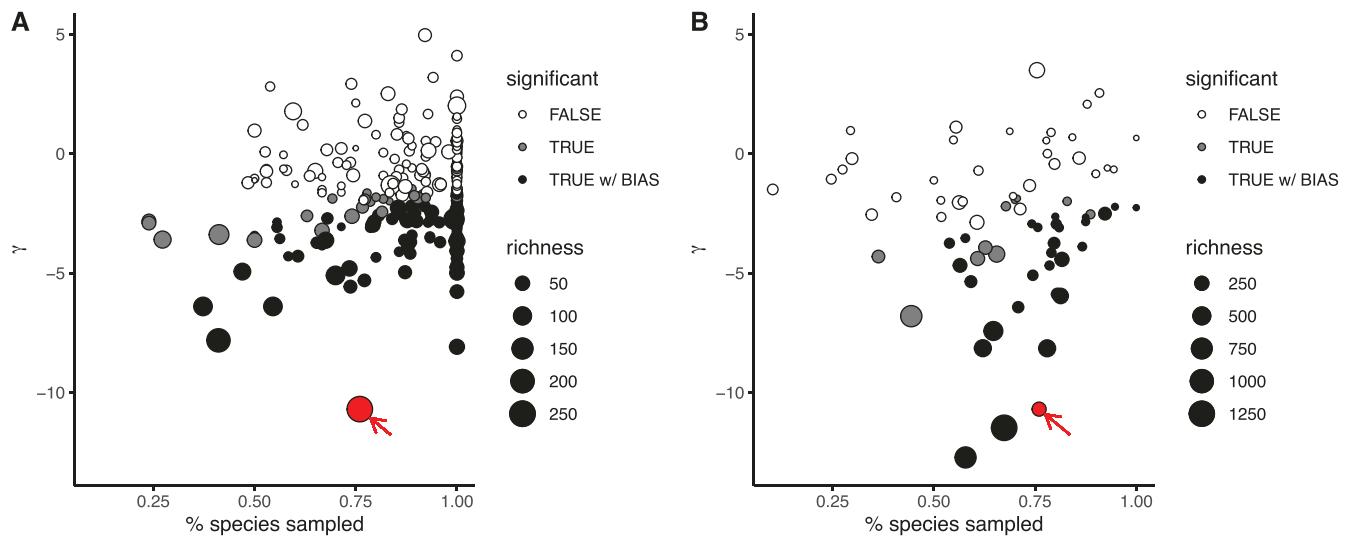


Figure 7. Early burst signal (gamma statistic: γ) in Australian sphenomorphines (red arrow) in relation to a compilation of published values (A) and across 71 subfamily-level clades of squamate reptiles (B). For A, we extracted γ values from the literature (see Supporting Information Table S3). For B, we calculated γ for squamate subfamilies with at least 10 sampled species using the phylogeny published in Title et al. (2024). We determined if γ was significant after accounting for unsampled species by simulation (significant = TRUE) using reported levels of taxon sampling for each clade. We then determined whether the computed γ values would remain significant if true species richness is underestimated (as would be expected under models of cryptic speciation and/or protracted speciation; significant = TRUE w/ BIAS). Here, we assumed a 10% increase in species richness due to unknown, unsampled species—for squamates, this is probably conservative (Melville et al. 2021). We further assumed that there was weak bias in sampling, such that unsampled tips were likely to be in the 50% of youngest divergences. Australian sphenomorphines have a markedly low γ value compared to other clades in both datasets. Across 71 subfamily-level squamate clades, only two (much larger) clades have γ values comparable to that observed for sphenomorphines: the Gekkoninae and Colubrinae. Many clades exhibit γ values that are probably robust to low levels of taxon murk. Note that increased cryptic diversity and/or phylogenetic sampling biases beyond the levels assumed here could further affect significance levels; these results should thus be treated provisionally.

Taxon murk and diversity patterns

With up to tenfold greater species richness at local and regional scales relative to physiographically comparable deserts elsewhere, the lizards of arid Australia have generated considerable ecological and evolutionary interest (Pianka 1972, 1986, Morton and James 1988, James and Shine 2000, Rabosky et al. 2011). Much work on this system has focused on sphenomorphines, because they comprise a substantial fraction of desert lizard diversity at both local and regional scales (Pianka 1969a, 2014, James and Shine 2000). One hypothesis for the exceptional richness of Australian lizard communities at biogeographical scales is that the tempo of species accumulation has been faster in these deserts, perhaps due to the dynamic physiography of the Australian arid zone from the Miocene to the present (Pianka, 1972; Byrne et al. 2008). This accelerated tempo could, in principle, be mediated either by faster rates of speciation, lower rates of extinction, or both. While extinction rates are notoriously difficult to estimate in the absence of dense fossil sampling (Quental and Marshall 2009, 2010, Rabosky 2010), phylogenetic studies suggest recent speciation rates in Australian lizards are comparable to those in other clades or desert regions (Tejero-Cicuéndez et al. 2022, Title et al. 2024).

Some have suggested that geographical heterogeneity in taxonomic practice—with some regions receiving more attention than others—could result in biased estimates of speciation rates and, in particular, lead to underestimates of speciation rates in

high-diversity regions (Freeman and Pennell 2021, Melville et al. 2021, Frateles et al. 2024, Tavares et al. 2024). In particular, if our studies of Australian desert lizards have undersampled many recent or cryptic speciation events, detecting a phylogenetic signal of rapid speciation would be difficult. However, we find no evidence that taxon murk can explain the slow to moderate tempo of speciation in the Australian deserts. At least for sphenomorphines, speciation rates under the operational delimitation scheme—which we consider the most plausible description of ‘true’ species-level diversity in the group—do not change appreciably relative to a morphological delimitation for the group (Fig. S5: blue versus magenta points). These results do not provide a positive explanation for the exceptional diversity of Australian lizards, but support the robustness of previous results rejecting the faster speciation hypothesis.

Speciation slowdown, incumbent advantage, and adaptive radiation

Nearly all analyses of the fossil record suggest an approximate equivalence between long-term averages of speciation and extinction rates (Marshall 2017), at least for most times and clades throughout Earth’s history. To the extent that extinction is phylogenetically random with respect to the pool of lineages in existence at any given time, it should rapidly erode the signal of early burst speciation from time-calibrated phylogenies (Pybus and Harvey 2000, Quental and Marshall 2009, Liow et al. 2010, Rabosky and

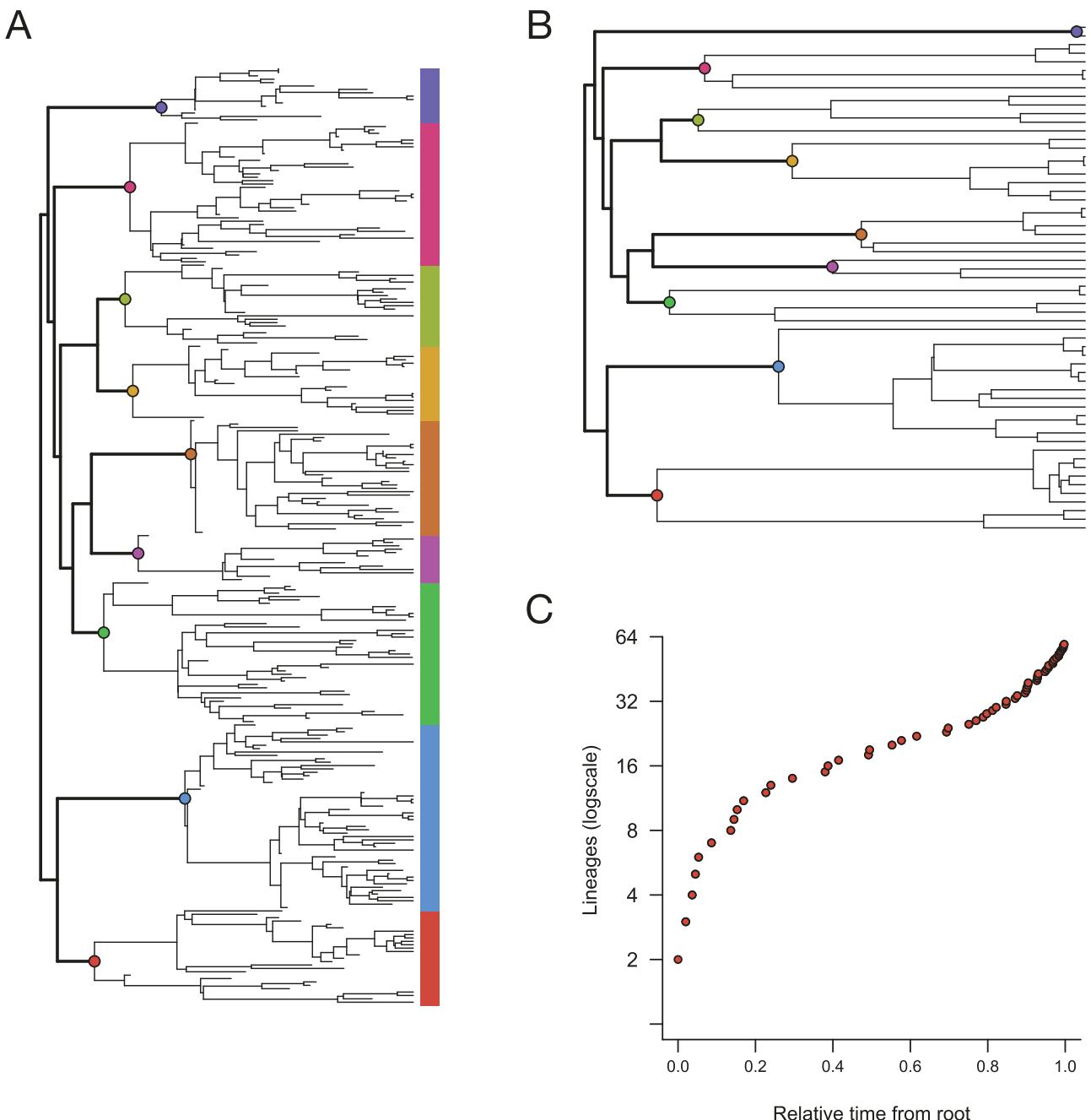


Figure 8. An incumbency effect during the early stages of evolutionary radiations facilitates persistence of early-diverging lineages, even when turnover rates are high. A, hypothetical phylogeny generated under a nearly balanced speciation–extinction process but where the first eight speciation events resulted in clades with incumbent advantage (see details below). Thus, each incumbent clade has some surviving descendants in the present day. Bold branches denote the incumbent ‘backbone’ of the phylogeny. Despite high turnover of species within these clades, the incumbency effect leads to low overall extinction probabilities for the clade as a whole (incumbent clades shown with distinct colours). B, reconstructed phylogeny for the comprehensive phylogeny shown in A, generated by simply pruning all extinct lineages, thus corresponding to an idealized molecular phylogeny with extant species only. Coloured nodes correspond to incumbent clades from A; note that incumbent backbone persists in the reconstructed tree. C, lineage-through-time plot for the reconstructed phylogeny. Note the apparent signal of early burst of speciation in this tree, driven by the persistence of early-diverging (incumbent) lineages. Compare the scenario shown in C to the observed lineage-through-time plot for Australian sphenomorphines (Fig. S5A), noting in particular the apparent deceleration in the rate of lineage accumulation during the first 0.25 relative time units. Details: phylogeny was constructed by simulating nine extant clades (i.e. with at least one surviving descendant) under a constant-rate birth–death process ($\lambda = 1$, $\mu = 0.95$). The ancestors of each clade were then joined sequentially through a random coalescence process, until all nine clades were joined in a common tree structure. While not a formal process-based simulation of the incumbency scenario, this algorithm ensured that at least some descendants of each of the initial eight splits in the tree persisted through the present day despite high turnover within each of the fully stochastic subtree simulations (i.e. the incumbent clades demarcated by distinct colours).

Hurlbert 2015). The fossil record suggests that we should place high prior odds against ever detecting early burst speciation patterns, even when clades have in fact diversified under a true early burst process. Thus, to us, the most surprising implication of a speciation slowdown in sphenomorphines is that such a signal is even detectable in our dataset.

We consider it highly unlikely that extinction rates have been low throughout the history of sphenomorphine diversification, given that there are few—if any—clades that experienced sustained diversification with little extinction (Marshall 2017). Assuming that the signal of early, rapid speciation is indeed robust, we can ask: what dynamics of extinction are consistent with the phylogenetic speciation patterns we observe? We propose an explanation that has largely been neglected in the recent literature: the prevalence of early burst speciation, in both sphenomorphines and other taxa, reflects the incumbent advantage associated with early diverging lineages during evolutionary radiations. The incumbent advantage hypothesis (also ‘priority effect’: Stroud et al. 2024) proposes that the descendants of early diverging lineages are afforded some degree of long-term extinction resistance when considered as a whole, perhaps due to their early occupancy of specific ecological ways of life or biogeographical zones (Rosenzweig and McCord 1991, Reijenga et al. 2021, Stroud et al. 2024).

For example, suppose that the sphenomorphine radiation involved early divergence into a number of distinct adaptive zones (Simpson 1944, Schlüter 2000). Incumbent advantage ensures that clades occupying such zones will rarely be replaced by lineages from other clades, regardless of the magnitude of lineage turnover within zones. Thus, even if extinction rates overall are high, the early diverging clades—the incumbents—rarely go extinct in their entirety, thus ensuring that the phylogenetic signal of those early divergences is retained in present-day time-calibrated phylogenies (Fig. 8). Incumbent advantage to early diverging clades can lead to apparent slowdowns in speciation even when speciation rates have been constant through time, provided that the early diverging clades have high extinction resistance. Some degree of incumbent advantage has already been recognized at the largest phylogenetic scales. As pointed out by Strathmann and Slatkin (1983), the persistence of early diverging animal phyla with few present-day species is highly improbable under simple models of diversification that lack some clade-wide property of extinction resistance. The present-day biota includes the descendants of many Cambrian (or earlier) divergences that, with high extinction-driven turnover, would have been unlikely to survive to the present in the absence of incumbent advantage. Our hypothesis is that a similar process operates during evolutionary radiations at shallower phylogenetic scales.

What are the ecological or biogeographical factors that could lead to early burst diversification during the radiation of Australia’s sphenomorphine skinks? Previous analyses have demonstrated that much of the variation in body shape in Australian sphenomorphines is partitioned among early diverging lineages and suggests a dramatic deceleration in the rate of shape evolution through time (Rabosky et al. 2014a), consistent with verbal models of adaptive radiation (Simpson 1944, Stroud and Losos 2016). In addition, sphenomorphine diversification is also biogeographically structured, and incumbent advantage for clades

diversifying within major ecogeographical regions could potentially lead to the observed early burst pattern of speciation. The arid and semi-arid regions of Australia, for instance, are thought to have formed ~20 Mya, leading to rapid radiations in many taxa including *Gossipium* grasses, pygopod geckos, and macropod marsupials (Byrne et al. 2008). These regions are also greatly enriched in *Ctenotus* and *Lerista* species, with relatively few representatives from other taxa. Conversely, many other genera (e.g. *Eulamprus*, *Hemiergis*, *Glaphyromorphus*) are concentrated in (respectively) mesic temperate woodlands, eastern highlands, and monsoonal tropics. Nonetheless, we consider any hypotheses about specific causes to be highly speculative, and there is as yet little compelling evidence that early branching events are associated with particular trophic resources, microhabitats, or other factors.

CONCLUSION

We have documented that key features of sphenomorphine skink diversification are robust to multiple forms of ‘taxon murk’ (Table 1). Most significantly, the radiation of this group is associated with a robust signal of early rapid speciation and cannot be explained by unsampled cryptic diversity or protracted speciation. At first glance, this pattern seems consistent with expectations under a Simpsonian model of adaptive radiation, and many researchers have interpreted such patterns as reflecting a response to ecological opportunity on a continental scale. However, there is a danger in constructing a causal narrative for sphenomorphine diversification that goes beyond the basic facts of diversification that we have presented here. As pointed out by Eldredge and Gould (1972), the ‘cloven hoofprint of theory’—those conceptual models we hold in our minds, prior to seeing the data—can shape our a posteriori interpretations in a way that extends beyond the facts at hand. There is a tendency to interpret diversification patterns in light of our paradigmatic notions of evolutionary radiations and their causes, particularly the adaptive versus nonadaptive dichotomy (Rundell and Price 2009) or the notion that radiations are aligned with key ecological or behavioural axes of divergence (Streelman and Danley 2003, Martin and Richards 2019).

At present, the facts are inadequate to determine whether these paradigms are sufficient to describe patterns of diversification in many large continental radiations, including the sphenomorphine skinks considered in our study. Much of our understanding of sexual selection in sphenomorphines—and intraspecific behaviour more generally—comes from just a single species, *Eulamprus heatwolei* (Noble et al., 2013; Van Dyke et al., 2021). With the exception of arid zone communities of just a single genus—*Ctenotus* (Pianka 1969b, James 1991, Goodyear and Pianka 2011, Rabosky et al. 2011)—we have very little comparative data on the ecology and demography of sphenomorphine taxa. Ecological interactions between species remain largely unknown, beyond generalizations based on proxy traits such as body size (Rabosky et al. 2007a), with this work also focused on *Ctenotus*. In addition, while limb reduction is clearly associated with fossoriality, our understanding of other aspects of the form–function–ecology relationship remain virtually unknown in the group. Our understanding of the basic biology and

ecology of sphenomorphines is, in our view, woefully inadequate for understanding how and why they became such a dominant clade in a land that is already home to numerous spectacular squamate radiations.

SUPPLEMENTARY DATA

Supplementary data are available at *Evolutionary Journal of the Linnean Society* online.

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AUTHOR CONTRIBUTIONS

Sonal Singhal (Conceptualization [Equal], Data curation [Equal], Formal analysis [Lead], Investigation [Lead], Methodology [Equal], Project administration [Equal], Resources [Equal], Visualization [Lead], Writing - original draft [Equal]), Ivan Prates (Conceptualization [Equal], Investigation [Equal]), Huateng Huang (Data curation [Equal], Investigation [Equal]), Maggie R. Grundler (Investigation [Supporting]), Alan R. Lemmon (Investigation [Supporting]), Emily Moriarty Lemmon (Investigation [Supporting]), Pascal O. Title (Investigation [Supporting]), Stephen C. Donnellan (Investigation [Supporting], Resources [Supporting]), Craig Moritz (Investigation [Supporting], Resources [Supporting], Resources [Supporting]), and Dan Rabosky (Conceptualization [Lead], Data curation [Equal], Funding acquisition [Lead], Investigation [Equal], Methodology [Equal], Project administration [Equal], Resources [Equal], Writing - original draft [Equal])

CONFLICT OF INTEREST

The authors have no conflict of interests to declare.

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DATA AVAILABILITY

Accession information for all new genomic data and previously published data is available in Table S1. All scripts used in analysis are available at <https://github.com/singhal/sphenophylo> and key data files (*Ctenotus leonhardii* genome, clade-level phylogenies, synthetic tree, and taxonomic framework phylogenies) are available at <https://doi.org/10.5281/zenodo.1393686>

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